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Hearing Research 178 (2003) 27–34

HEARING RESEARCH

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Hearing in American leaf-nosed bats. II: *Carollia perspicillata*

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Received 29 August 2002; accepted 23 December 2002

Abstract

We determined the audiograms of two short-tailed fruit bats (*Carollia perspicillata*), 18-g phyllostomids from Central and South America. For testing, we used a conditioned suppression/avoidance procedure with a fruit juice reward. At an intensity of 60 dB SPL, the hearing of *C. perspicillata* extends from 5.2 to 150 kHz, showing a best sensitivity of 0 dB at 25 kHz and a secondary region of sensitivity at 71 kHz. Although *C. perspicillata* is frugivorous and therefore does not rely on sonar for detecting and pursuing insects, its audiogram is similar to that of insectivorous bats; similarly, there is no suggestion of unusual sensitivity associated with its low-intensity echolocation calls. The behavioral audiogram is compared to previously published physiological estimates of hearing.

Key words: Audiogram; Chiroptera; Echolocation; Evolution; Mammal; Evoked potential

1. Introduction

This report is the second in a series examining the passive hearing of New World neotropical bats in the highly diverse and successful family, Phyllostomidae. In our first report on a phyllostomid, the greater spear-nosed bat, *Phyllostomus hastatus*, we found that its good high-frequency hearing, restricted low-frequency hearing, and overall sensitivity were not unusual but instead fit the pattern seen in other small mammals (Koay et al., 2002a,b). Indeed, so far there are no clear differences between the frequency limits and best sensitivity of bats as a group and those of most other mammals (Heffner et al., 2001a,b; Koay et al., 1998). However, behavioral audiograms are available for very few of the approximately 800 species of echolocating bats, and a larger and broader sample of bats is needed to determine whether some features of their passive hearing reflect their specialization for echolocation.

We report here the audiogram of the short-tailed fruit bat, *Carollia perspicillata*, a small (18 g) frugivorous and nectarivorous phyllostomid whose behavior and physiology have been previously studied (Cloutier and Thomas, 1992; Fleming, 1988). This species is of particular interest because the hearing of a small microchiropteran frugivore has yet to be examined, despite the success of this lifestyle and the abundance of such species in the Neotropics. *C. perspicillata* is a solitary feeder, agile flyer, and forages in relatively cluttered areas low in the canopy where it is less exposed to predators (Bonaccorso and Gush, 1987). It use olfaction for detection and initial location of ripe fruit, but then uses echolocation for the final approach to the fruit, with vision apparently playing little role (Thies et al., 1998). The echolocation calls of *C. perspicillata* consist of short, frequency-modulated signals that contain several harmonics. Like many phyllostomids, *C. perspicillata* is considered to be a ‘whispering’ bat, as its echolocation pulses are 40–60 dB less intense than those of aerial insectivores such as *Myotis lucifugus* (Griffin, 1958; Howell, 1974). Although its low-intensity sonar may reduce the range at which objects can be detected, *C. perspicillata* is as adept at detecting and avoiding fine suspended wires as insectivorous bats

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0378-5955/03/$ – see front matter © 2003 Elsevier Science B.V. All rights reserved.
doi:10.1016/S0378-5955(03)00025-X

that use more intense sonar signals, possibly because of their extreme agility (Griffin and Novick, 1955; Grinnell and Griffin, 1958).

We determined the behavioral audiograms of two *C. perspicillata* using the same conditioned suppression/avoidance procedure previously used with the greater spear-nosed bat (*P. hastatus*), big brown bat (*Eptesicus fuscus*), and the Egyptian fruit bat (*Rousettus aegyptiacus*) (Koay et al., 1997, 1998, 2002a,b). We also obtained evidence that the secondary peaks of sensitivity in the mid-range of its hearing, often seen in the behavioral audiograms of mammals in general and bats in particular, are strongly influenced by the directionality of the pinnae. Finally, we compared the hearing ability of this species to that of other mammals, and examined the relationship of the behavioral audiogram to neural response thresholds at different levels of the auditory system.

2. Materials and methods

Using the conditioned suppression/avoidance procedure, a hungry bat was trained to lick a reward spout in order to receive a steady trickle of fruit juice. A pulsing tone was then presented at random intervals and followed by a mild shock at its offset. The bats learned to avoid the shock by breaking contact with the spout whenever they detected the signal. Thresholds were determined by successively reducing the intensity of the tone until the bats could no longer detect it above chance.

2.1. Subjects

The colony of *C. perspicillata* was maintained in captivity on a diet of mixed fruit (see Barnard, 1995). Two 1–2-year-old captive-born bats were tested (a male and female, designated A and B, respectively). While on test they were individually housed in wood and plastic mesh cages (48×39×95 cm) and allowed to fly daily in the test chamber. They had free access to water and received food during the test sessions, with additional fruit supplements as required to maintain healthy weight. The use of animals in these experiments was approved by the Institutional Animal Care and Use Committee of the University of Toledo.

2.2. Behavioral apparatus

Testing was conducted in a carpeted, double-walled acoustic chamber (IAC model 1204; 2.55×2.75×2.05 m), the walls and ceiling of which were lined with acoustic foam. The equipment for stimulus generation and behavioral measurement was located outside the chamber and the bats were observed via closed-circuit television.

The bats were tested in a cage (37×22×23 cm) constructed of 0.5-in (1.26 cm) hardware cloth, and raised 93 cm above the floor on a tripod (for a drawing of the test cage, see Koay et al., 2002a). A vertical reward spout (2 mm diameter brass tube, topped with a 4×6 mm oval lick plate attached at a 45° angle) projected 7 cm above the cage floor at the front of the cage. The spout was attached via flexible tubing to a 10-cc glass syringe that served as the fruit juice reservoir. Fruit juice (a mix of cantaloupe, pear juice, and vitamin supplement, finely blended and sieved) was dispensed using a syringe pump housed in a high-density polyethylene box (64×21×28 cm). To eliminate the noise of the pump, the box was lined with acoustic foam and placed on the floor behind the test cage.

During testing, a bat climbed onto a small platform (13×7×7 cm) located directly behind the reward spout. The tip of the reward spout was placed 1 cm in front of the bat at platform height so as to eliminate obstructions between the animal's ears and the loudspeaker while it ate from the spout. The platform was covered with a piece of dampened carpet to provide traction and facilitate electrical contact with the bat. A contact circuit, connected between the food spout and platform, was used to detect when an animal made contact with the spout and to activate the syringe pump. Requiring the bat to maintain mouth contact with the spout also served to keep its head in a fixed position within the sound field.

A shock generator was connected between the reward spout and platform. The shock was adjusted for each individual to the lowest level that produced a reliable avoidance response, which consisted of backing away slightly from the spout or lifting and turning the head. A 25-W shock-indicator light, placed 0.5 m below the cage, was turned on and off with the shock to signal a successful avoidance and indicate when it was safe to return to the spout.

2.3. Acoustical apparatus

Sine waves were generated by a signal generator (Zonic A&D 3525 for frequencies from 4 to 100 kHz, or Krohn-Hite 2400 AM/FM Phase Lock Generator for frequencies from 100 to 160 kHz) and continuously monitored using a frequency counter (Fluke 1900A). The tones were pulsed (Coulbourn S53-21, 400 ms on and 100 ms off, for four pulses) and routed through a rise–fall gate (Coulbourn S84-04, 10 ms rise-decay). The signal was then bandpass filtered (Krohn-Hite 3202, ±1/3-octave bandpass centered on the test frequency, 24 dB/oct rolloff) and the intensity attenuated (Hewlett Packard 350D) as needed for threshold determinations.

Finally, the signal was amplified (Crown D75 or Adcom GFA545), monitored for distortion with an oscilloscope, and routed to a loudspeaker in the test chamber. The loudspeaker was placed approximately 1 m in front of the cage (0° elevation and azimuth), facing the bat when it was eating from the spout.

Various loudspeakers were used to present the tones: for 4 kHz either a 12-in (30.4 cm) or 6-in (15.2 cm) woofer was used; for frequencies from 5 to 160 kHz, one of two ribbon tweeters (Panasonic EAS-10TH-400C) was used. Thresholds were obtained at the following frequencies: 4, 5, 6.3, 8, 12, 16, 25, 32, 40, 45, 50, 56, 64, 71, 80, 90, 100, 110, 125, 140, and 160 kHz. To determine the effect of sound source elevation on hearing sensitivity, thresholds at selected frequencies were also obtained for Bat B with the loudspeaker placed 30° above and below the horizon.

2.4. Sound level measurement

The sound pressure level (SPL re 20 μNewton/m^2) for frequencies of 100 kHz and below was measured daily with a 1/4-in (0.64-cm) microphone (Brüel and Kjaer 4939, corrected for free-field with the protection grid on), preamplifier (Brüel and Kjaer 2669), and measuring amplifier (Brüel and Kjaer 2608). For measuring frequencies above 100 kHz, a 1/8-in (0.32-cm) microphone (Brüel and Kjaer 4138, corrected for free-field with the protection grid on) was used. Sound level measurements were taken by placing the measuring microphone in the position normally occupied by a bat's head and ears while it ate from the spout and pointing it directly at the loudspeaker (0° orientation). Measurements taken throughout the area occupied by a bat's head and pinnae showed a relatively homogeneous sound field (±1 dB), indicating that there were no significant standing waves, nodes, or reflections that might affect threshold. The output of the measuring amplifier was then routed to a spectrum analyzer (Zonic A&D 3525) to check the speaker output for distortion. Any harmonics present were at least 40 dB below the fundamental and below the threshold of the bat at that frequency.

2.5. Behavioral procedure

The bats were tested daily during the early evening hours when they were normally active after approximately 20 h of food deprivation. A hungry bat was initially trained to climb onto the platform and lick the food spout to receive a slow but steady trickle of fruit juice. Requiring the bat to make mouth contact with the spout also served to fix its head in the sound field and orient it toward the loudspeaker. A pulsing tone was then presented at random intervals, followed at its offset by a mild electric shock (300 ms duration, ≤ 1.25 mA) delivered between the spout and platform. The bat learned to avoid the shock by breaking contact with the spout whenever it heard a tone. The shock was adjusted for each animal to the lowest level that reliably produced an avoidance response to a clearly audible signal. The shock was considered mild, as the bats readily returned to the spout to resume eating after the shock had been delivered (indicated by the offset of the shock-indicator light).

Test sessions were divided into 2-s trials, separated by 1.5-s intertrial intervals. Approximately 22% of the trial periods contained a pulsing tone (warning signal), whereas the remaining trial periods were silent (safe signal). The contact circuit was used to detect whether the bat was in contact with the spout during the last 150 ms of each trial. If it broke contact for more than half of the 150-ms response period, a detection response was recorded. This response was classified as a hit if the trial had contained a tone (i.e., a warning signal) or as a false alarm if the trial had been silent (i.e., a safe signal). Blocks of six to eight warning trials (along with approximately 24–32 associated safe trials) were given at each stimulus intensity, and the hit and false alarm rates were then determined. Finally, the hit rate was corrected for false alarms to produce a performance measure (Heffner and Heffner, 1995) according to the formula: performance = hit rate − (false alarm rate × hit rate). This measure proportionately reduced the hit rate by the false alarm rate associated with each intensity (i.e., each block of trials) and varied from 0 (no hits) to 1 (100% hit rate with no false alarms).

Auditory thresholds were determined by reducing the intensity of the tone in successive blocks of six to eight warning trials until the bat no longer responded to the warning signal above chance (i.e., the hit and false alarm rates did not differ significantly; $P > 0.05$, binomial distribution). Note that the shock level was initially adjusted to ensure that the bats were performing at optimal levels as indicated by near perfect performance when the signal was clearly audible. At intensities close to threshold, the false alarm rates increased to about 20%, indicating that the bats remained motivated to avoid the shock. Threshold was defined as the intensity at which the performance measure equaled 0.50, which was usually obtained by linear interpolation. Testing was considered complete at a particular frequency when the thresholds obtained in at least three different sessions were within 3 dB of each other and showed no further improvement. Once an audiogram had been completed, thresholds for selected frequencies were rechecked to ensure reliability. Data from early sessions before the animals were well-practiced observers were not included in the final threshold averages.

3. Results

In a typical test session lasting approximately 1.5–2 h, each bat consumed up to 9 ml of juice – enough to permit presentation of 40–50 warning trials (together with 160–200 safe trials) and to determine a threshold for a single frequency. Because their natural fruit diet is relatively low in nutrients, this species must consume a larger volume of food than it can ingest in one feeding bout (Gardner, 1977). Thus each session included at least two bouts of feeding, with 20- to 30-min pauses in between, during which the food cleared their digestive system.

The audiograms of the two *C. perspicillata* are illustrated in Fig. 1. The mean values for each bat after the thresholds had reached asymptote (three thresholds within a range of ±3 dB) are listed in Table 1. The two individuals showed good agreement, as is expected for young, healthy, and well-motivated animals of the same species. Beginning with a mean threshold of 72 dB at 4 kHz, the audiogram shows a comparatively rapid improvement in sensitivity up to 25 kHz, the frequency of best hearing, with a mean threshold of 0 dB SPL. Hearing sensitivity then steadily decreased to 36.5 dB at 50 kHz but improved again as frequency further increased to 71 kHz, forming a secondary peak of sensitivity with an average threshold of 16.5 dB. Above 71 kHz, sensitivity again declined slowly with increasing frequency up to 125 kHz (29 dB), then steeply to 80 dB at 160 kHz, the highest frequency tested. At an intensity of 60 dB SPL, *C. perspicillata* can hear frequencies from 5.2 kHz to 150 kHz, a range of 4.85 octaves.

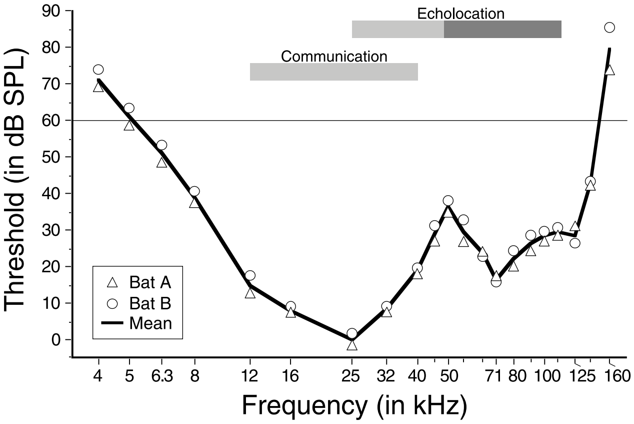

Fig. 1. Audiograms of two *C. perspicillata*. A and B represent individual bats. Darker shading indicates the dominant second and third harmonics of their echolocation call and the frequencies of their communication calls. Lighter shading indicates the weaker first harmonic in their echolocation call. The horizontal line at 60 dB SPL indicates the range of frequencies audible at 60 dB.

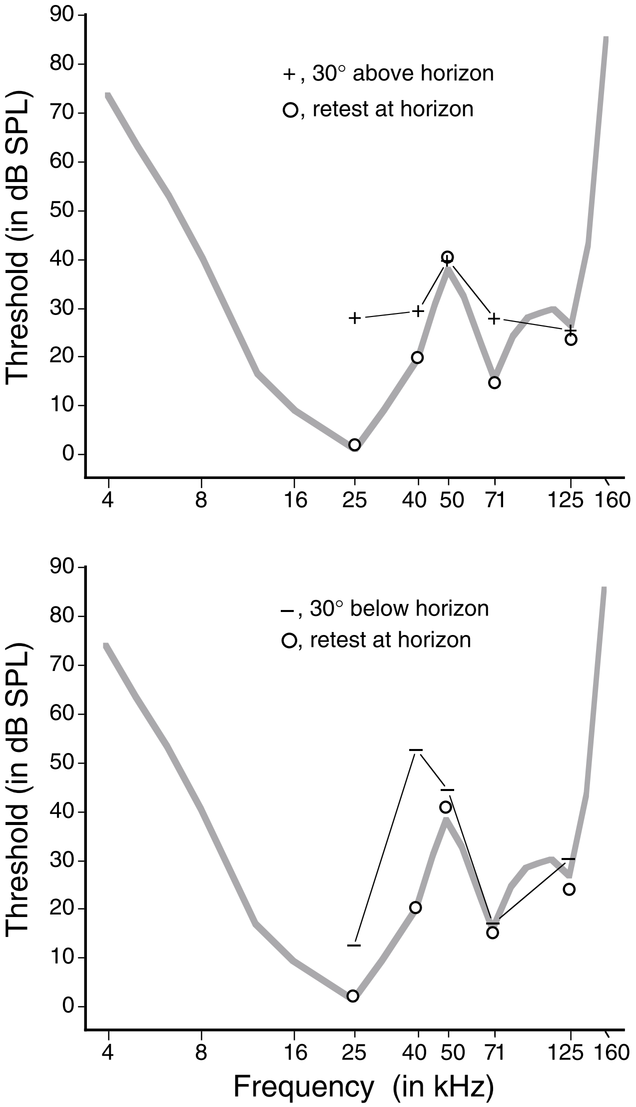

Fig. 2. Raising or lowering the sound source relative to the pinnae for Bat B changed the magnitude and position of the secondary peaks of sensitivity and insensitivity in the mid-range of the audiogram. Retesting with the sound sources at the horizon confirmed the bat's original thresholds.

To explore the possibility that the decrease in sensitivity centered at 50 kHz may have been due to pinna directionally, additional thresholds at 25, 40, 50, 71, and 125 kHz were determined at different sound source elevations in the median sagittal plane for Bat B (Fig. 2). *Elevating* the sound source 30° above the horizon did not improve detectability at 50 kHz (the peak of insensitivity), but did decrease detectability by 10–27 dB at flanking frequencies of 25, 40, and 71 kHz. As a result, the sharp peak in the audiogram became less prominent. *Lowering* the sound source 30° below the horizon enhanced the insensitivity peak and shifted it slightly from 50 to 40 kHz. Whereas detectability of sound sources located 30° below the horizon decreased by as much as 32 dB at 40 kHz (compared to thresholds at horizon), sensitivity at 25, 50, and 71 kHz decreased

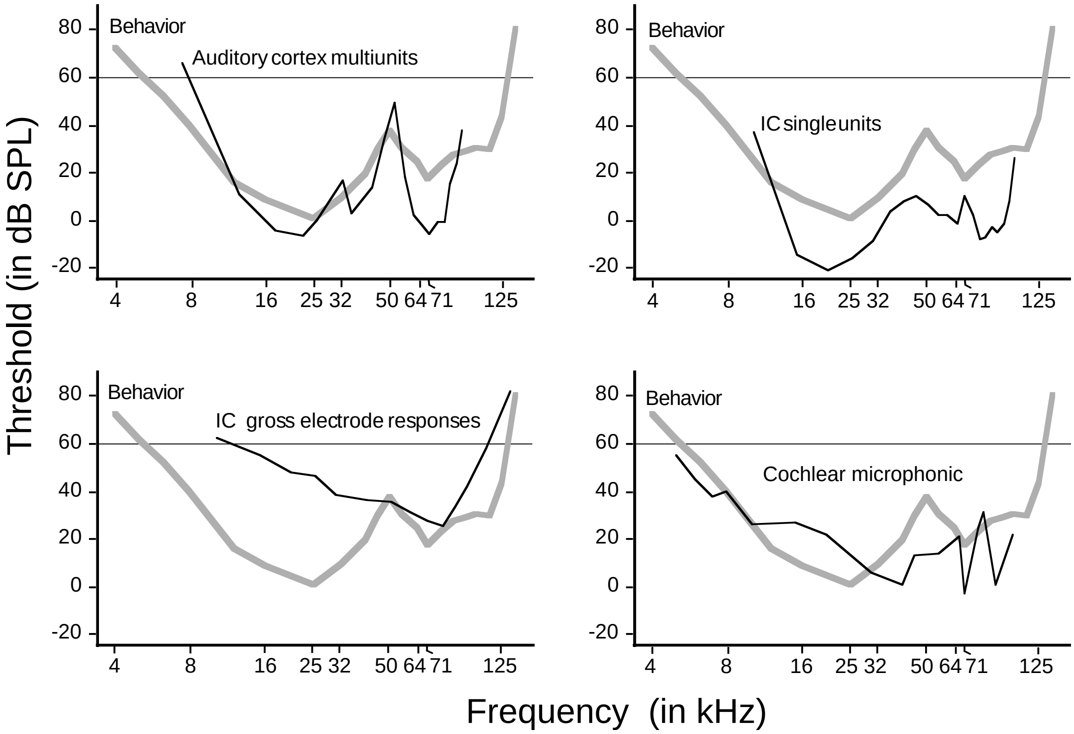

Fig. 3. Comparison of behavioral and four neural audiograms for *C. perspicillata*. Behavioral audiogram shown in gray, neural audiograms shown in black. Auditory cortex multiunits from Esser and Eiermann, 1999; IC (inferior colliculus) single units from Sterbing et al., 1994; IC gross electrode responses from Grinnell, 1970; cochlear microphonic recording from Howell, 1974. Thin horizontal line indicates 60 dB SPL.

by less than 10 dB. At 125 kHz, the highest frequency tested, neither raising nor lowering the sound source affected the thresholds. This limited change in threshold at high frequencies is supported by direct measures of pinna directionality in this species, in which 30° changes in elevation near the midline resulted in changes in amplitude of less than 5 dB at the tympanic membrane for frequencies of 45 kHz or higher (Jen and Chen, 1988).

The differences in threshold as a function of elevation cannot be attributed to variation in the animals' performances over time, as re-testing with the speakers at the horizon (0° elevation) produced thresholds that differed by no more than 2.5 dB from the original (see Fig. 2). Thus, the systematic changes in thresholds at different speaker elevations suggest that the irregular shape of the audiogram in the mid-frequency range is largely a result of the filtering characteristics of the pinnae at these frequencies.

4. Discussion

4.1. Auditory sensitivity

The best sensitivity of *C. perspicillata* is 0 dB (at 25 kHz), which is near to 2.9-dB mean for best sensitivity among terrestrial mammals. It is also within the range of the best sensitivity of other bats, which extends from −16 dB in the Indian false vampire (*Megaderma lyra*; Schmidt et al., 1983/1984) to 10 dB in the little brown bat (*M. lucifugus*; Dalland, 1965). Thus, *C. perspicillata*, like the related *P. hastatus* (Koay et al., 2002a), show no unusual sensitivity for detecting their low-intensity sonar calls. Instead, it is likely that these species and other whispering bats use low-intensity calls to reduce the echo clutter from dense vegetation in the leaf canopy (Schnitzler and Henson, 1980; Schnitzler and Kalko, 1998; Simmons and Stein, 1980).

The frequencies to which *C. perspicillata* is most sensitive correspond closely to the frequencies involved in mother–young communication, approximately 12–40 kHz (Gould, 1975; Sterbing, 2002). A similar observation has been made for *P. hastatus* (Bohn et al., 2001). These frequencies are below the frequencies used for echolocation and well below the upper limits of hearing. Although it is conceivable that the audiogram evolved to match the frequencies at which infants vocalize, it is equally plausible that infants evolved to vocalize at the frequencies to which their mothers are most sensitive. Other than constraints on sensitivity imposed by background and physiological noise, little is known about the selective pressures that influence best sensitivity in mammals. Nevertheless, it does appear that the most sensitive part of the hearing range in bats is not necessarily associated with echolocation.

C. perspicillata has a secondary region of sensitivity from 56 to 125 kHz that corresponds to the dominant second and third harmonics of its echolocation call (sweeping from 80 to 48 kHz and from 112 to 80 kHz, respectively; Gould, 1977; Grinnell, 1970; Pye, 1966). The reduced sensitivity in the range of its weak first harmonic (sweeping from 50 to 25 kHz) was shaped in part by pinna directionality, as it could be altered by changing the elevation of the sound source relative to the pinnae (Fig. 2). The increased thresholds seen here following both raising and lowering the speaker are in accord with physical measures of pinna directionality in this species (Jen and Chen, 1988) that show greater amplitudes when the sound source is at or near the horizon. These spectral transformations of sound by the pinnae generate pinna cues known to be especially important for localizing sound sources in the vertical plane (e.g., Lawrence and Simmons, 1982; Middlebrooks and Green, 1991; Roffler and Butler, 1968; Wotton et al., 1996; Wotton and Jenison, 1997).

4.2. High- and low-frequency hearing limits

C. perspicillata has very good high-frequency hearing. Its high-frequency hearing limit (the highest frequency audible at 60 dB SPL) is 150 kHz, the highest so far reported for a bat or for any other mammal that hears in air. The ability to perceive such high frequencies has implications for the study of auditory mechanisms. For example, the cochlear amplifier must either be capable of functioning at higher frequencies than previously thought (Gale and Ashmore, 1997), or else is not necessary for hearing these frequencies.

Although it may seem that the excellent high-frequency hearing of *C. perspicillata* is due to its use of echolocation, it should be noted that when functional head size is taken into account, neither *C. perspicillata* nor any other bat has unusually good high-frequency hearing. Good sensitivity to high frequencies is common in small mammals because of the selective pressure to detect high frequencies for use in passive sound localization. This selective pressure on passive hearing applies to all mammals studied so far, except those that do not localize sound (Heffner and Heffner, 1993). Small mammals must hear frequencies that are effectively shadowed by their small heads and pinnae in order to produce interaural intensity/spectral differences and monaural pinna cues large enough to be effective indicators of locus (Heffner and Heffner, 1998; Masterton et al., 1969). Thus, mammals with small interaural distances, including bats and aquatic mammals (whose interaural distances are functionally small because of the faster travel time of sound in water), are under selective pressure to hear frequencies high enough to be useful in sound localization. Among mammals, there is a high correlation between functional head size (the time required for a sound to travel from one auditory meatus to the other) and the highest frequency audible at 60 dB ($r = -0.787$, $P \leq 0.0001$), and *C. perspicillata* does not deviate significantly from this relationship ($t = 1.49$, $P = 0.142$, two-tailed). However, although the hearing of *C. perspicillata* is consistent with the selective pressure for passive sound localization that applies to all mammals, it is not impossible that it has been slightly extended by selective pressure for echolocation. Indeed a goal of this series of studies is to determine if the evolution of echolocation in bats has imposed additional selective pressure to hear higher frequencies than non-echolocating mammals.

In contrast to its excellent high-frequency hearing, *C. perspicillata* has very restricted low-frequency hearing – at a level of 60 dB it hears only as low as 5.2 kHz. So far, among mammals, only fishing bats (*Noctilio leporinus*; Wenstrup, 1984) and little brown bats (*M. lucifugus*; Dalland, 1965) with low-frequency limits of 7.5 and 10.3 kHz, respectively, have poorer low-frequency hearing. Far from being unusual, an *in*ability to hear frequencies below 500 Hz is found in about one third of the nearly 70 species of mammals tested so far, with the remaining mammals hearing below 125 Hz (for the distribution of low-frequency hearing in mammals, see Heffner et al., 2001a). We have suggested elsewhere that this dichotomy in the distribution of mammalian low-frequency hearing may be a reflection of differences in the mechanisms used in pitch perception, with species that do not hear low frequencies relying only on a place code for pitch (Heffner et al., 2001a). We also raised the possibility that hearing low frequencies may be a disadvantage in some circumstances – for example, processing low-frequency information might interfere with the processing of information carried in high frequencies, including returning echoes (Koay et al., 2002b).

4.3. Comparison with neural estimates of hearing

The auditory system of *C. perspicillata* has been the subject of several electrophysiological investigations, including the determination of thresholds of auditory neurons for sounds of different frequencies. It is of interest to compare these neural thresholds with the behavioral audiogram. Fig. 3 illustrates how four physiological measures compare with behavioral sensitivity. As can be seen, each of the physiological audiograms shows some similarity to the behavioral audiogram. Although the curve derived from multiunit recordings in auditory cortex (Esser and Eiermann, 1999) reflects the general shape of the behavioral audiogram, sensitivity of the animal is overestimated at some frequencies. Sensitivity is similarly overestimated throughout much of the audible range by the curve based on single units in the inferior colliculus (Sterbing et al., 1994).

These overestimates are likely due to differences in sound calibration and the orientation of the pinnae, as well as to the use in physiological studies of tones with abrupt onsets that generate additional frequencies (sometimes referred to as 'spectral splatter'). The remaining two curves showed less similarity to the behavioral audiograms. Whereas the gross electrode recordings from the inferior colliculus (Grinnell, 1970) reflect *C. perspicillata*'s high-frequency sensitivity, they underestimate low-frequency sensitivity despite using a stimulus configuration selected to elicit the lowest thresholds. The cochlear microphonic recording (Howell, 1974) parallels the low- and mid-frequency thresholds but becomes erratic at high frequencies. Neither the gross electrode responses nor the cochlear microphonic revealed the decreased sensitivity near 50 kHz.

In analyzing these differences, it should be noted that it is unlikely that they are due to individual differences in hearing. Barring malformation and disease, the hearing of a species is relatively uniform, even in the case of separate breeding populations as with different breeds of dogs (Heffner, 1983). The important point is that no simple adjustment, such as raising or lowering thresholds by a constant amount or shifting the audiograms higher or lower on the frequency scale, brings electrophysiological thresholds into good agreement with behavioral thresholds throughout the hearing range. Of particular importance for comparisons across species is the inability of electrophysiological measures to depict accurately the upper and lower limits of hearing. Thus, although electrophysiological measures can provide some estimate of an animal's hearing ability, they cannot substitute for measures of the capacity of the whole animal to respond to sound, and this is the ability that is subject to natural selection. Because the ultimate goal of physiology is to understand neural mechanisms underlying hearing, it is essential to avoid the temptation to substitute physiological measures for the behavioral functions they hope to explain.

Acknowledgements

Supported by NIH grant R01 DC02960.

References

Barnard, S.M., 1995. Bats in Captivity. Wild Ones Animal Books, Springfield, CA.

Bohn, K.M., Moss, C.F., Wilkinson, G.S., 2001. Audio-vocal matching in greater spear-nosed bats. Bat Res. News 42, 144–145.

Bonaccorso, F.J., Gush, T.J., 1987. Feeding behaviour and foraging strategies of captive phyllostomid fruit bats: An experimental study. J. Anim. Ecol. 56, 907–920.

Cloutier, D., Thomas, D.W., 1992. *Carollia perspicillata*. Mamm. Species 417, 1–9.

Dalland, J.I., 1965. Hearing sensitivity in bats. Science 150, 1185–1186.

Esser, K.-H., Eiermann, A., 1999. Tonotopic organization and parcellation of auditory cortex in the FM-bat *Carollia perspicillata*. Eur. J. Neurosci. 11, 3669–3682.

Fleming, T.H., 1988. The Short-Tailed Fruit Bat, a Study in Plant–Animal Interactions. The University of Chicago Press, Chicago, IL.

Gale, J.E., Ashmore, J.F., 1997. An intrinsic frequency limit to the cochlear amplifier. Nature 389, 63–66.

Gardner, A.L., 1977. Feeding habits. In: Baker, R.J., Jones, J.K., Carter, D.C. (Eds.), Biology of Bats of the New World Family Phyllostomatidae. Part II. Special Publications of the Museum, Texas Tech University. Texas Tech Press, Lubbock, TX, pp. 293–350.

Gould, E., 1975. Neonatal vocalizations in bats of eight genera. J. Mammal. 56, 15–29.

Gould, E., 1977. Echolocation and communication. In: Baker, R.J., Jones, J.K., Carter, D.C. (Eds.), Biology of Bats of the New World Family Phyllostomatidae. Part II. Special Publications of the Museum, Texas Tech University. Texas Tech Press, Lubbock, TX, pp. 247–279.

Griffin, D.R., 1958. Listening in the Dark: The Acoustic Orientation of Bats and Men. Yale University Press, New Haven, CT.

Griffin, D.R., Novick, A., 1955. Acoustic orientation of neotropical bats. J. Exp. Zool. 130, 251–300.

Grinnell, A.D., 1970. Comparative auditory neurophysiology of neotropical bats employing different echolocation signals. Z. Vgl. Physiol. 68, 117–153.

Grinnell, A.D., Griffin, D.R., 1958. The sensitivity of echolocation in bats. Biol. Bul. 114, 10–22.

Heffner, H.E., 1983. Hearing in large and small dogs: Absolute thresholds and size of the tympanic membrane. Behav. Neurosci. 97, 310–318.

Heffner, H.E., Heffner, R.S., 1995. Conditioned avoidance. In: Klump, G.M., Dooling, R.J., Fay, R.R., Stebbins, W.C. (Eds.), Methods in Comparative Psychoacoustics. Birkhäuser, Basel, pp. 73–87.

Heffner, H.E., Heffner, R.S., 1998. Hearing. In: Greenberg, G., Haraway, M. (Eds.), The Encyclopedia of Comparative Psychology. Garland, New York, pp. 290–303.

Heffner, R.S., Heffner, H.E., 1993. Degenerate hearing and sound localization in naked mole rats (*Heterocephalus glaber*), with an overview of central auditory structures. J. Comp. Neurol. 331, 418–433.

Heffner, R.S., Koay, G., Heffner, H.E., 2001a. Audiograms of five species of rodents: Implications for the evolution of hearing and the encoding of pitch. Hear. Res. 157, 138–152.

Heffner, R.S., Koay, G., Heffner, H.E., 2001b. Sound localization in a New-world fruit bat, *Artibeus jamaicensis*: Acuity, use of binaural cues, and its relationship to vision. J. Acoust. Soc. Am. 109, 412–421.

Howell, D.J., 1974. Acoustic behavior and feeding in glossophagine bats. J. Mammal. 55, 293–308.

Jen, P.H.-S., Chen, D., 1988. Directionality of sound pressure transformation at the pinna of echolocating bats. Hear. Res. 34, 101–118.

Koay, G., Heffner, H.E., Heffner, R.S., 1997. Audiogram of the big brown bat *Eptesicus fuscus*. Hear. Res. 105, 202–210.

Koay, G., Heffner, R.S., Heffner, H.E., 1998. Hearing in a megachiropteran fruit bat, *Rousettus aegyptiacus*. J. Comp. Psychol. 112, 371–382.

Koay, G., Bitter, K.S., Heffner, H.E., Heffner, R.S., 2002a. Hearing in American leaf-nosed bats. I: *Phyllostomus hastatus*. Hear. Res. 171, 97–103.

Koay, G., Heffner, R.S., Bitter, K., 2002b. Hearing in the greater spear-nosed bat, *Phyllostomus hastatus*: Audiogram, temporal integration, sound localization, and use of binaural cues. Assoc. Res. Otolaryngol. Abstr. 25, 210.

Lawrence, B.D., Simmons, J.A., 1982. Echolocation in bats: The external ear and perception of the vertical position of targets. Science 218, 481–483.

Masterton, B., Heffner, H., Ravizza, R., 1969. The evolution of human hearing. J. Acoust. Soc. Am. 45, 966–985.

Middlebrooks, J.C., Green, D.M., 1991. Sound localization by human listeners. Annu. Rev. Psychol. 42, 135–159.

Pye, A., 1966. The structure of the cochlea in Chiroptera III. Microchiroptera: Phyllostomatoidea. J. Morphol. 121, 241–254.

Roffler, S.K., Butler, R.A., 1968. Factors that influence the localization of sound in the vertical plane. J. Acoust. Soc. Am. 43, 1255–1259.

Schmidt, S., Turke, B., Volger, B., 1983/1984. Behavioural audiogram from the bat, *Megaderma lyra*. Myotis 21–22, 62–66.

Schnitzler, H.-U., Henson, O'D.W., 1980. Performance of airborne animal sonar systems: I. Microchiroptera. In: Busnel, R.-G., Fish, J.F. (Eds.), Animal Sonar Systems, Plenum Press, New York, pp. 109–181.

Schnitzler, H.-U., Kalko, E.K.V., 1998. How echolocating bats search and find food. In: Kunz, T.H., Racey, P.A. (Eds.), Bat Biology and Conservation. Smithsonian Institution Press, Washington, DC, pp. 183–204.

Simmons, J.A., Stein, R.A., 1980. Acoustic imaging in bat sonar: Echolocation signals and the evolution of echolocation. J. Comp. Physiol. A 135, 61–84.

Sterbing, S.J., 2002. Postnatal development of vocalizations and hearing in the phyllostomid bat, *Carollia perspicillata*. J. Mammal. 83, 516–525.

Sterbing, S.J., Schmidt, U., Rubsamen, R., 1994. The postnatal development of frequency-place code and tuning characteristics in the auditory midbrain of the phyllostomid bat, *Carollia perspicillata*. Hear. Res. 76, 133–146.

Thies, W., Kalko, E.K.V., Schnitzler, H.-U., 1998. The roles of echolocation and olfaction in two Neotropical fruit-eating bats, *Carollia perspicillata* and *C. castanea*, feeding on *Piper*. Behav. Ecol. Sociobiol. 42, 397–409.

Wenstrup, J.J., 1984. Auditory sensitivity in the fish-catching bat, *Noctilio leporinus*. J. Comp. Physiol. A 155, 91–101.

Wotton, J.M., Jenison, R.S., 1997. The combination of echolocation emission and ear reception enhances directional spectral cues of the big brown bat, *Eptesicus fuscus*. J. Acoust. Soc. Am. 101, 1723–1733.

Wotton, J.M., Haresign, T., Ferragamo, M.J., Simmons, J.A., 1996. Sound source elevation and external ear cues influence the discrimination of spectral notches by the big brown bat, *Eptesicus fuscus*. J. Acoust. Soc. Am. 100, 1764–1776.